SOME REMARKS WITH REGARD TO PROFESSOR BOURNE'S MONOGRAPH ON THE NERITIDÆ.

By Dr. H. Simroth.

Read 12th November, 1909.

We owe many thanks to Professor Bourne for his most accurate study of the interesting family of the Neritidæ.[1] It is in no way my intention to criticize any of the many facts brought forward by him. But as I think I can give in several directions another interpretation, which may perhaps clear up the various difficulties he finds in the problem, I ask for permission to do so.

Professor Bourne unites all the forms of the great family in one genus, *Nerita*, which he divides into the four sections *Nerita*, s.s., *Paranerita*, *Septaria*, and *Neritina*. Here I may remark that Schepman[2] divides the group into two families, Neritacea and Neritilidæ, on conchological characters, the Neritilidæ comprising the genera *Neritilia* and *Septaria*. I should prefer the anatomical division of Bourne. As it is founded in the first place upon the genital organs I will begin with those.

Professor Bourne has had only female individuals of *Septaria*, but both sexes of all the other genera. I think I can explain the cause of the absence of males. When I once had a series of about thirty specimens of an undetermined species of *Septaria*, all the large individuals proved to be females, the males being small, only about half the diameter. Therefore it may be presumed that in this genus the males are dwarfed. Future investigation will have to decide whether the genus is hermaphroditic and proterandrous, developing first the male and afterwards the female organs, as is the case with many Pulmonata, or if the proterandric condition was a character of a hypothetical ancestor, the sexes being individually separated as at present.

I will now give the explanation of the compound structure of the genitalia. They differ widely from all Prosobranchs. But I do not find any difficulty in comparing them with those of the Pulmonata. Professor Bourne regards the ovary and the testis, the oviduct and the sperm-duct, as homologous organs. I shall endeavour to explain the homologies as completely as possible.

Female Organs.

Bourne uses the very good expression 'ootype' for uterus, thus indicating the descent from the Platodes. It is the female part of the Pulmonata—sperm-oviduct or uterus. The vitelline gland

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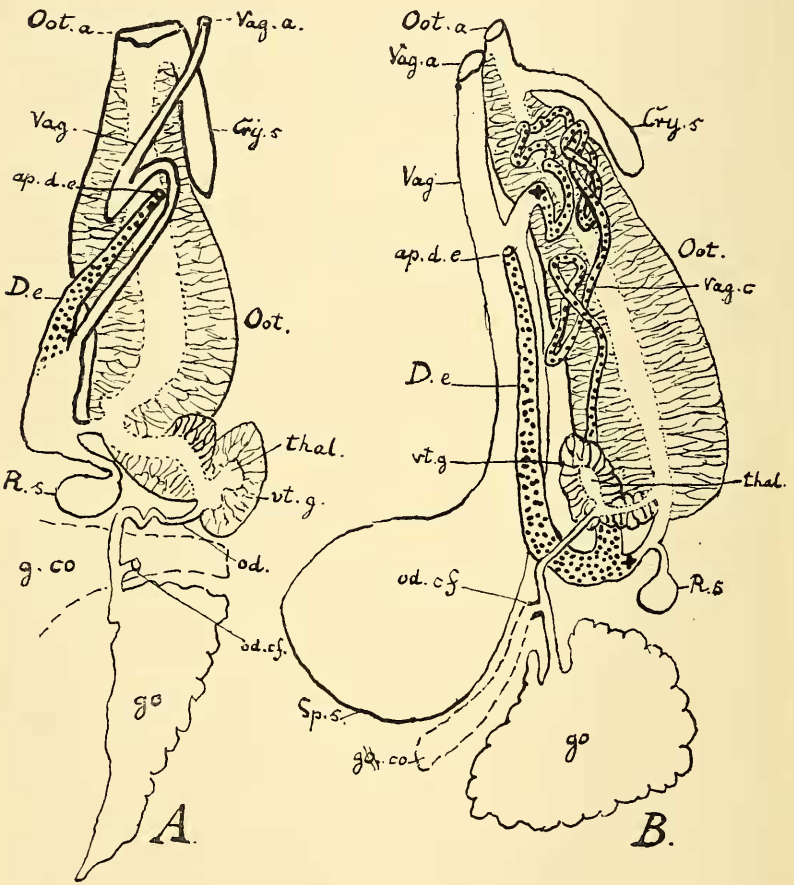
[1] G. Bourne, "Contributions to the Morphology of the group Neritacea of Aspidobranch Gastropods." Part I: The Neritidæ. Proc. Zool. Soc. London, 1908, pp. 810-87, pls. xlvi–lxvi, and 1 text-fig.

[2] M. M. Schepman, "The Prosobranchia of the Siboga-Expedition." Part I: Rhipidoglossa and Docoglossa.

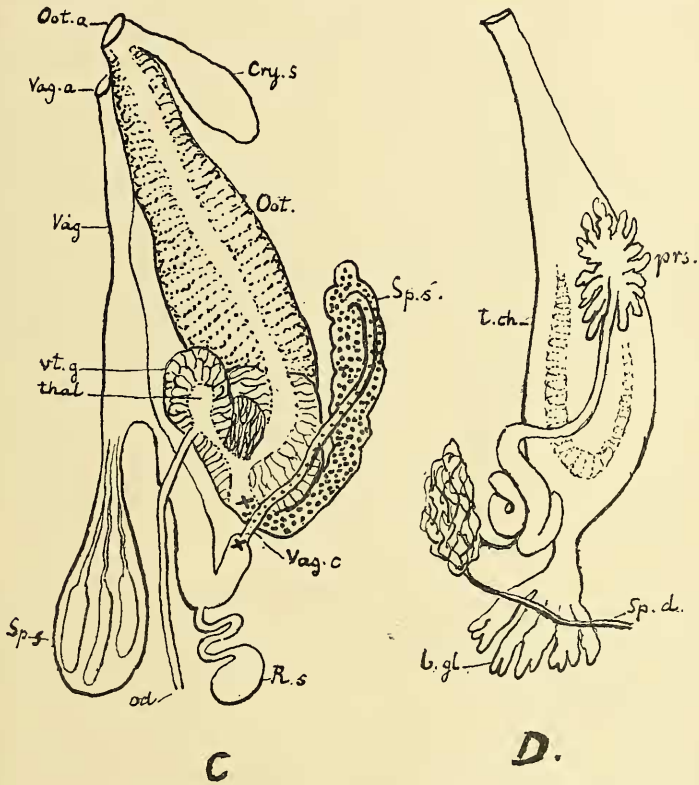
(*vt.g.*) is the albumen gland of authors. The other glands of the ootype are highly differentiated, more than in the Pulmonata. This is in connexion with the more complicated spawn. In the Stylommatophora there is only the egg-shell, in the Basommatophora the eggs are bound together by mucus, but in the Neritidæ the spawn is enclosed in a firm capsule, needing a new glandular differentiation for itself, as I have already pointed out in the Bronn Mollusca.



Bourne thinks that the crystal sac is a shell-gland, the chalk concretions of it being applied in forming the spawn capsule, but this is a hypothesis without observation, as he says himself. In my opinion the crystal sac is only a Pulmonate dart-sac, which ceased to act when the terrestrial ancestors were submerged under water.

A little chalk is still secreted in the common form of calco-sphærites, but no dart is formed.

The vagina is the same as in the Pulmonata. The receptaculum seminis is the bursa copulatrix, which is also named receptaculum by many authors. The sperm-sac or spermatophore-sac of *Paranerita* and *Nerita* (Figs. B and C, *Sp.s.*, but not Fig. C, *Sp.s'.*) is a secondary dilatation or a secondary bursa copulatrix. It is smaller in the true freshwater forms *Septaria* and *Neritina*, in *Neritina* being the smallest.



The cause of the dilatation and of its differences seems to be the following. In the terrestrial ancestor there was transferred in copulation *one* spermatophore, as in nearly all Pulmonata. The first tropical forms that invaded the sea, i.e. *Nerita*, and in a second degree *Paranerita* (for this see below), conserved the spermatophore, but transferred in one copula not one spermatophore but a number together (Fig. C). Whilst one spermatophore has room enough in the bursa or receptaculum (*R.s.*), the space is too narrow for the passing of several together; therefore the secondary bursa is formed

by dilatation (*Sp.s.*). *Septaria*, and especially *Neritina*, stayed in the fresh water, *Neritina* going farthest northward; in this way *Neritina* was adapted in the highest degree to the new conditions, it lost the spermatophore, transferring the sperm freely. Accordingly there no sperm-sac or secondary bursa is formed. The connecting canal between the receptaculum and thalamus is also to be found in the Opisthobranchia, e.g. *Aplysia* (= *Tethys*, Pilsbry). Many Pulmonata have the remains of it in the diverticulum. For this is sometimes, as shown by Semper, connected with the upper end of the sperm-oviduct at the point where the albumen gland is inserted.

There is still to be explained the enigmatic duct of *Septaria* (Fig. A), the enigmatic duct and vaginal canal of *Paranerita* (Fig. B), and the organs which Professor Bourne indicates in *Nerita* (Fig. C, *Vag.c.* and *Sp.s'.*) all roughly dotted in my figures. The latter should not be so designated, the real sperm-sac being the bursa sperm-sac. All these things seem to be new formations, founded on mechanical causes. The bursting open and evacuation of the spermatophore is connected with a certain swelling or a kind of explosion, as I found once in *Arion*. The bursting of several spermatophores at the same time must augment the pressure, and the vaginal aperture being closed by muscular effort the pressure must take another way. It creates the enigmatic duct of *Septaria* (A), and the long vaginal canal and enigmatic duct of *Paranerita* (B). But in *Nerita* the dilatation and prolongation take place between the bursa or receptaculum and the thalamus. Therefore the vaginal canal and secondary sperm-sac of *Nerita* (Fig. C, *Vag.c.* and *Sp.s'.*) are not strongly homologous to the dotted organs in Figs. A and B, but homodynamic, as founded on the same functional causes. In Figs. B and C I have indicated the points between which the prolongation has taken place by a cross (+). By joining the two points the normal disposition would be given.

Male Organs.

The great prolongation of the sperm-duct is not rare in Pulmonata, e.g. *Vaginula* and *Oncidium*, as well as the dilatation of the sperm-duct or hermaphrodite duct in the distal part. Yet the prostate has always another aspect, for its tubes are inserted along the long sperm-oviduct, sometimes at intervals, as in *Agriolimax* or *Vitrina*. But take off the oviducal part of it, or uterus, and the tubes will approach as in *Nerita* (Fig. D, *prs.*). Spermatophores being formed, the terminal chamber (*t.ch.*) is nothing else than the epiphallus, and the basal gland is a flagellum. Its splitting up into many branches is not unparalleled, e.g. in *Agriolimax*.

It is quite uncertain if the cephalic penis was originally joined with the genital aperture by an inner vas deferens or an outer sperm groove, for we have to go back to a very old and primitive stock.

Other Organs.

Back to such a stock points also the oviduco-cœlomic funnel, discovered by Bourne. Perhaps he is not right in concluding that the genital canal must have been the right nephridium, for the use

of the cœlomic or pericardial ducts as nephridia is already a secondary function. Nierstrasz[1] has lately shown that the Solenogastres possess these ducts, but without excretory functions.

In the same way the question arises whether there is only the left ctenidium or also the remains of a right one. In my opinion the ctenidia are secondary acquisitions on the margin of the mantle, as in *Valvata*, the typical hermaphrodite freshwater Prosobranch. In one species of *Pleurotomaria* Bouvier found in the hind part of the mantle-cavity a typical network of blood-vessels as in the Pulmonate lung, the ctenidia being restricted to the outer parts. *Valvata* shows that the right ctenidium is already vanishing before it enters into the mantle-cavity itself. Therefore I think it uncertain whether the right ctenidium in *Nerita* was once fully developed or not. Perhaps the rudimentary right ventricle of the heart is a proof of the full development in the ancestors. Professor Bourne has given a valuable description of the nervous system. He demonstrates that the pedal ganglia are rounded organs, and that there are no transverse commissures between the pedal nerves. The pleural ganglia are joined by a short commissure with a ganglion therein, as in many Pulmonata. And even the absence of the supra-intestinal nerve in *Neritina* connects their form more closely with the Pulmonata.

Other organs, e.g. the radula, can be taken in the same sense. The rhipidoglossate radula is a highly differentiated one, whereas many Pulmonata, e.g. *Ostracolethe*,[2] possess an equally large number of denticles, but all of the same simple form. The stomach has a diverticulum, homologous to the spiral cæcum of many Aspidobranchs. Its absence in *Neritina* is in accordance with its higher systematic position (see above). The same diverticulum we find in the Cephalopoda, but not less in the Aplysiidæ,[3] where it is described as liver cæcum; and I may add that among the Pulmonata one species of *Hyalimax* possesses the same organ, whereas it is wanting in others, agreeing with what we find in the Neritidæ. The cæcum is the sign of great antiquity, which is lost in the progress of development. The nephridium of the Neritidæ, as described by Professor Bourne, is composed of an excretory part and of a non-excretory part. He avoids naming the latter part ureter, because it is not a straight duct. But have we not such ureter forms in many Pulmonata, e.g. *Limax* and *Arion*?

The Geographical Distribution.

Given the similarity of most of the organs of the Neritidæ to the Pulmonata, we may ask whether the Pulmonata are derived from the Neritidæ or the Neritidæ from the Pulmonata. Perhaps the

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[1] H. F. Nierstrasz, "Die Amphineuren": Ergebnisse und Fortschritte der Zoologie, herausgeg. von Spengel, Bd. i, Heft ii.

[2] Simroth, Zool. Anz., vol. xxv, p. 62.

[3] F. M. MacFarland, "The Opisthobranchiate Mollusca of the Branner–Agassiz Expedition to Brazil"; Leland Stanford, jun., Univ. Publications, Univ. Series II, 1909.

majority of zoologists would be inclined to derive the Pulmonata from the Neritidæ in accordance with the common view that the marine forms were the precursors of the terrestrial. My opinion is the reverse with regard to most cases, and chiefly to the present one. The formation of spermatophores is only the exception among the Prosobranchia, it is the rule among the Pulmonata. Therefore[1] the probability is that the Pulmonata are the older stock. The same is proved by the single spermatophore and the typical bursa copulatrix in the Pulmonata, whereas the several spermatophores and the secondary bursa testify the derived character of the Neritidæ.

All this is in accordance with the geographical distribution in connexion with the pendulation theory.[2] Professor Bourne regards the tropical marine *Neritæ* as the oldest stock. But he cannot find its ancestors. He considers the Helicinidæ, the nearest allies of the Neritidæ, as a young group, because they are not found in a fossil state. Therefore he thinks that the similarity of the Palæozoic *Dawsonella* with the Helicinidæ is founded only upon convergence, and not upon true affinity. Why not? I do not think the palæontological argument can demonstrate the contrary. If I am right, between the Palæozoic Pupæ and the modern living forms we have the same gap. And this is not surprising, as terrestrial animals have not so good a prospect of being preserved in a fossil state as aquatic ones. The geographical distribution of the Helicinidæ is a most striking argument for their age. They inhabit two separated areas, in the east and in the west. *Dawsonella* demonstrates that they once lived in our European–North American quadrant, when we were in a more southern position. By the pendulating movement directed northward, they were obliged to retire into the areas of the east and west poles with a constant tropical climate, where we find them to-day. The old Neritidæ were also originally tropical terrestrial forms, but during the same pendulating movement they retired into the sea with its more equal temperature, and acquired one or two gills, or they retired into fresh water, the freshwater forms being those which were more able to adapt themselves to diminishing temperature during the northward movement under the swinging circle, as the conditions of fresh water conform more to those of the soil. The old freshwater stock was changed to *Paranerita*, and in the torrents to *Septaria*. When the pendulating movement transferred their area further northward, they retired into the warmer parts of the globe. One part became submerged under sea-level, another stayed in fresh water, *Septaria* retiring into the east pole area occupying the former under-ridges from Ceylon to Mauritius, and through the Pacific to the coral islands. The allied *Pileolus* of the Secondary age seems to prove that even this stock originated in Europe. Finally, that part which persisted for the longest time in fresh water, and became adapted to the lowest temperature, losing in the meantime the faculty of

[1] H. Simroth, "Die Entstehung der Landtiere"; Leipzig, 1891.
[2] H. Simroth, "Die Pendulationstheorie"; Leipzig, 1907.

forming spermatophores,[1] is *Neritina*, but even the most northern living species, *N. fluviatilis*, is at the present time invading the sea in the Baltic on its northern confines under the swinging circle.

[1] I consider the transferring of the sperm by one spermatophore of the Pulmonata as the primary state, and the several spermatophores of *Nerita* as the secondary. Here it could be objected that the Cephalopoda in copulation behave in the same manner as *Nerita*. But I should remark that I have tried to derive also the Cephalopoda from an old terrestrial Pulmonate stock. The palæontological appearance of the different Cephalopoda groups is in full agreement with the pendulation theory.